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The Morphology of the Genus Viola*

BY HENRY KRAEMER

A few years ago the author undertook, at the suggestion of Professor Arthur Meyer, Marburg, Germany, the study of the two forms of *Viola tricolor* L., which are rather common in certain parts of Germany, with the view of this study forming the basis of a scientific monograph on the genus *Viola*. The great necessity for such a work is expressed in Engler and Prantl's "Die natürlichen Pflanzenfamilien" as a "dringende Notwendigkeit."

The writer has examined and compared certain parts of about 30 species of this genus, most of which are found in the United States. Special attention has been devoted to the character of style and stigma, stamen, hairs upon stigma, stamens and petals, shape and size of pollen grains and bracts with mucilage-secreting hairs. The results of the study thus far made are given at this time with the reservation to change certain details as further study may suggest, since there is so much chaos in the genus that one hesitates to make positive statements with regard to the characters of the different species.

CHARACTERS OF THE GENUS.

The genus is characterized, so far as the writer's studies go, by herbaceous, annual, biennial or perennial plants, which are either caulescent or acaulescent. Stolons or rhizome-like products may be present or absent. The arrangement of the leaves in the acaulescent forms is basal, whereas in the caulescent, they are alternate, the disposition above the cotyledons varying from $\frac{1}{4}$ and $\frac{1}{3}$ to $\frac{2}{5}$. The leaves, apparently in all cases, consist of lamina, petiole and stipulae. The lamina, stipulae, bracts and calyx all appear to possess characteristic mucilage-secreting hairs at the apex and at the apices of the divisions.† On the stem, lamina, stipulae, bracts and all parts of the flower excepting the stamens, characteristic sub-epidermal mucilage cells are to be found.

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* Read at the annual meeting of the Society for Plant Morphology and Physiology, Dec. 28, 1898.

† Already described in Inaugural-Dissertation on *Viola tricolor* L. Marburg, 1897.

The flowers are solitary and arise in the axils of the leaves, beginning normally with about the sixth node. The peduncle varies in length and bears at the summit the flower in a partly resupinate position. The length of peduncle increases from the development of the flower bud to the maturing of the fruit. The position of the flowers varies from an erect (in the bud) to a partly resupinate (in the full grown flower) and finally in the maturing of the fruit resumes the erect position. On the peduncle are borne the bracts which vary in size and in position to some extent on the same plant.

The flower consists of five sepals, five petals, five stamens and a one-celled ovary with three parietal placentae. There is an irregularity in form of stamens and petals and the flower is median zygomorphous. The sepals are green, equal and are provided at the base with a slight auriculate appendage. They are united with the ovary for about a third of the length of the latter and are persistent with the mature fruit.

The petals are of three kinds in shape, two above alike, two on each side alike and one that has a spur or sac-like appendage at the base. The latter petal is situated on the under side of the flower in its more or less resupinate position and is adnate with two of the sepals. The side petals are erect at the lower portion and bent so as to form with the spurred petal the characteristic short tube of the corolla. The side and spurred petals may be provided on the upper surface with papillae or hairs or both but are in some cases free from the same. The uppermost petals are similar in shape, nearly erect and resemble the upper portion of the side petals. Hairs are wanting but papillae are sometimes present.

In color the petals vary from a white (which may be streaked with purplish or brownish colored veins) to pale blue with darker colored veins, or deep blue or bluish-yellow or yellow color.

The petals and stamens are inserted on the calyx. The stamens alternate with the petals and lie close upon the ovary. They are connivent and are all provided at the apex with a yellowish arrow-shaped appendage. The two on the side near the spurred or sac-like petal possess in addition a sac-like or spurred nectar secreting appendage which projects into the petal. The anther cells are introrse and possess a characteristic collenchymatic thickened cell in the mesophyll. After fertilization and the development of the fruit the slight filament attaching the stamens to the calyx is ruptured.

The ovary is half superior, about 3 to 4 mm. long and possesses three parietal placentae on each of which 15 to 24 ovules are borne which are arranged in about four transverse rows. The odd one of the three carpels lies between the two spurred stamens. In some cases as in *V. odorata* and *V. scabriuscula* the ovary is covered with hairs.

The style is hollow, is either bent or straight, of either nearly uniform thickness or becoming gradually of greater diameter towards the apex. It is persistent and scarcely projects above the appendages of the stamens. The stigma is more or less head-like and hollow, in some cases of scarcely greater diameter than the style. In most cases it is, however, much larger and provided with a beak-like extension which projects in the direction of the petals and stamens, that have a sac-like or spurred appendage, and possesses at the apex an opening for the entrance of the pollen grains. There is also in some cases a posterior projection which may be quite prominent as in *V. palustris* and *V. primulaefolia.*

The fruit is a tricarpellary capsule discharging its seeds in dry weather by a sudden dehiscence.

The seeds are elliptical in shape (17 × 9 mm.) and when ripe of a yellowish-brown color; they possess a slight caruncle.

STIGMA IN DETAIL.

In the following species slight papillae are found on the outer surface of the stigma: *V. arenaria, V. blanda, V. lanceolata, V. odorata, V. ovata, V. palustris, V. pedata, V. primulaefolia, V. obliqua, V. palmata, V. rostrata, V. rotundifolia, V. sagittata, V. Selkirkii, V. sororia and V. striata.*

Both papillae and hairs are present on the outer surface of the stigma in the following: *V. Canadensis, V. delphinifolia, V. heterophylla, V. hastata, V. Labradorica, V. lutea, V. Nuttallii, V. pubescens, V. scabriuscula, V. striata, V. tricolor* and its varieties and *V. tripartita.*

A more or less developed lip-like appendage at the opening of the stigma is found in *V. heterophylla*, *V. lutea* and *V. tricolor* and its varieties.

STYLE IN DETAIL.

The length of style varies from 1.8 mm. (in *V. lutea*) to 3.9 mm. (in *V. pedata*). In the following species there is a decided bend in the style near the base: *V. Canadensis*, *V. hastata*, *V. lutea*, *V. heterophylla*, *V. rotundifolia*, *V. Nuttallii*, *V. scabriuscula*, *V. tricolor* and its varieties and *V. tripartita*. The following possess a slight bend in style: *V. arenaria*, *V. blanda*, *V. palustris*, *V. renifolia*, *V. delphinifolia*, *V. palmata*, *V. obliqua* and *V. odorata*.

In the following species the style is nearly straight: *V. pedata*, *V. sororia*, *V. striata*, *V. Selkirkii*, *V. Labradorica*, *V. rostrata*, *V. ovata*, *V. lanceolata*, *V. primulaefolia* and *V. sagittata*. The shape of style and stigma of the species examined is given in the figures.

STAMEN IN DETAIL.

The length of sac-like or spurred nectar-secreting appendage is in the following species from 0.9 mm. to 1.3 mm. in size and less than anther cells: *V. lanceolata*, *V. palustris*, *V. renifolia*, *V. blanda* and *V. primulaefolia*.

In the following species the spur is from 1.8 to 2.6 mm. in width and same length as anther cells: *V. hastata*, *V. Nuttallii*, *V. Canadensis*, *V. rotundifolia*, *V. scabriuscula*, *V. pubescens* and *V. tripartita*.

In the following species the spur extends below the anther to the distance in mm. indicated in the figures in parenthesis: *V. tricolor arvensis* (1.5), *V. ovata* (1.5), *V. pedata* (1.8), *V. tricolor vulgaris* (2.0), *V. palmata* (2.3), *V. arenaria* (2.6), *V. heterophylla* (2.6), *V. Labradorica* (2.6), *V. sororia* (2.6), *V. striata* (2.6), *V. lutea* (2.8), *V. obliqua* (2.8), *V. sagittata* (2.8), *V. delphinifolia* (3.0), *V. Selkirkii* (3.1), *V. odorata* (3.6), *V. rostrata* (9.3).

In the following species papillae are not found on anther cells but only upon the nectar-secreting spur; *V. arenaria*, *V. Canadensis*, *V. lanceolata*, *V. odorata*. In addition to the presence of papillae on the spur the following possess long (100 μ) hairs with a slight crook at the end on anther cells: *V. heterophylla*, *V. lutea*, and *V. tricolor* and its varieties. The remaining possess only papillae in both spur and the anther cells.

The pollen grains when dry are of a narrow elliptical shape and when examined in liquids are broadly elliptical or somewhat spherical. When viewed in section they are 4- or 5-sided. In the following species they are about 70 μ in diameter: *V. heterophylla*, *V. lutea* and *V. tricolor* and its varieties. In the remaining species examined they vary from 30 to 42 μ in diameter.

PETALS IN DETAIL.

Among writers there is considerable variance as to the presence or absence of hairs on the petals of the different species of this genus. This may be explained in part owing to the fact that at the portion of the petals where hairs are usually found (viz. at the opening of the corolla tube) large masses of germinating pollen grains, with their tubes matted together, are frequently seen and these might be easily mistaken for hairs without closer study. Hairs only occur upon the upper surface of the side and spurred petals and vary in form and size from minute papillae to long straight or corkscrew-like forms. On the petal with a sac-like or spur appendage no hairs or papillae are found in the following species: *V. striata*, *V. arenaria*, *V. blanda*, *V. hastata* and *V. Labradorica*. In the following species straight hairs varying from 3.5 to 5.2 mm. are found: *V. delphinifolia*, *V. obliqua* and *V. ovata*. In the following species characteristic corkscrew-shaped hairs, which vary in size from 2.5 to 5.2 mm., occur: *V. heterophylla*, *V. lutea*, and *V. tricolor* and its varieties. In the remaining species examined papillae are present.

On the side petals no hairs or papillae are found in *V. blanda*. In the following species papillae only are to be found: *V. lanceolata*, *V. palustris*, *V. pedata*, *V. primulaefolia*, *V. renifolia*, *V. rostrata*, and *V. Selkirkii*. In a few species the papillae appear to be either wanting or minute, hairs being present: *V. arenaria*, *V. Labradorica*, *V. odorata*, *V. ovata* and *V. sororia*. In the remaining species examined both papillae and hairs are to be found.

MUCILAGE CELLS.

The sub-epidermal mucilage cells have been shown by the author (*loc. cit.*) to be characteristic for the genus *Viola*, and possibly for some other genera of the group Violeae of the

Violaceae. This would distinguish the group from the Rinoreae and possibly Papayroleae, although of the latter no specimens have been examined.

The peculiarity in shape of these mucilage cells was considered by the author for some time as having in themselves a diagnostic specific value. But in only a few instances is this the case and further study is necessary here.

A CONSIDERATION OF SOME PROMINENT CHARACTERS OF THE GENUS.

For the full comprehension of the significance of the various parts of the plants of a genus and the value to be given to their similarity or dissimilarity in structure, considerable study must necessarily be given to many plants from rather widely separated areas.

1. As we look upon this genus we find that whether we are dealing with annuals, biennials or perennials, climatic influences play an important part, as Kerner has shown that where annuals do not have sufficient warmth to produce seeds (as in Alpine regions) the plants are transformed into perennials.

2. As to whether plants are caulescent or acaulescent the results of Kerner, as well as the author's own observations, would lead us to believe that they are dependent largely also on climatic conditions. Kerner found that the number and length of internodes that plants produced are dependent on the climate in which they are growing. Some plants of *Viola tricolor* L., var. *vulgaris* Koch which were gathered in October, 1895, on the top of an exposed mountain near the Struth Forest in Germany, were exceedingly dwarfed in every particular and resembled but slightly caulescent plants. On planting them in garden soil they become a foot high and in every way showed a stronger development.

3. Some species produce an addition to the spring flowers, cleistogamic flowers. It is not unusual for some plants in other orders to produce in the fall or late summer months cleistogamic flowers. These are produced when the grass and various other plants have grown up and the spring flowers would very likely, at this time, be passed unnoticed by the insects which might assist in their fertilization. This would correspond to the investigations of

Kerner upon *V. sepincola.* He found that this plant produced cleistogamic flowers only when growing in shaded woods and that the same plants when exposed to the sunshine produced beautiful blue and scented blossoms. This is possibly due to the fact, as he suggests, that when exposed to the sun bees will visit the flowers which they would not do if the plants were growing in dark woods.

4. In some plants, as in *V. hastata*, the rhizomes are frequently light-colored, approaching white. It would seem, further, according to Kerner, that such rhizomes were produced in these plants only when growing in dark recesses and well covered with soil, for if the plants are exposed to greater light these rhizomes become violet-colored. This would indicate that color of rhizome, like the previous characters, means simply a characteristic that is dependent upon situation or habitat.

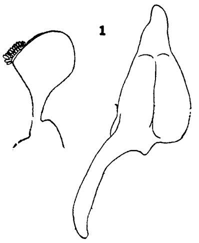
5. What value shall we place upon colors in flowers? Kerner has shown that when *V. calcarata* grows in the meadows of the western Central Alps that the flowers are of a blue color, whereas when growing in the Tyrolese Vintschigan they are yellow and when found on plants in the limestone mountains of Hungary they are violet-colored. It would seem from all observations that a number of factors are at work in producing colors in plants and that they are dependent upon conditions upon which we know very little.

6. The presence of hairs upon stigma, anther cells, side and spurred petals have possibly some significance when taken in connection with the shape of style (whether straight or with a knee-like bend) and length of spur of anther in assisting us to ascertain certain facts in the developmental history of this genus. Kerner considers that a style that is bent or deflexed is a device for impeding the progress of the insect into the flower so that all of the stamens are moved by the insect touching the 2-spurred ones and that the proboscis of the insect is thus covered with pollen. We would, therefore, conclude that in flowers with a straight style we have plants that are less differentiated and not so old in point of development. In this connection it is necessary, however, to consider also the development of hairs upon petals, stamens and stigma. Were these developed to impede, likewise, the progress

of beneficial insects or were they developed in the first place to keep out rain or injurious insects? The position of the flower (more or less resupinate) would indicate that the former is accomplished by this means alone. As to whether the plant first perfected all its parts for inducing cross fertilization and then produced other developments for protection from injurious influences, etc., are questions upon which a further morphological study of the genus will undoubtedly throw some light.

CLASSIFICATION OF THE GENUS.

I. From the observations made by the author up to the present time it would appear that one group is distinguished from all others by possessing a nearly globular stigma with a more or less lip-like appendage; a style with a knee-like bend in the lower portion; long hairs on the stamens and corkscrew-shaped hairs upon the spurred petal; the spur of the stamen is 2.0–2.8 mm. in length. This group comprises *V. heterophylla* (Fig. 4), *V. lutea* (Fig. 3), *V. tricolor vulgaris* (Fig. 1), *V. tricolor arvensis* (Fig. 2).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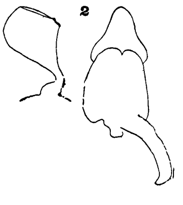
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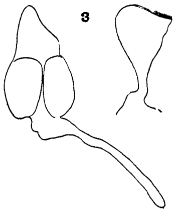
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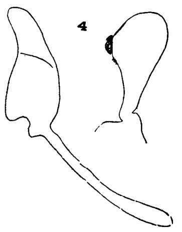
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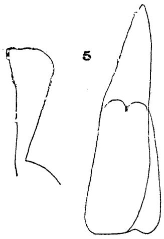
II. The remaining species are characterized by a stigma that is slightly greater in diameter than the style or is somewhat globular with a beak-like projection at the apex of which the opening for the entrance of the pollen grains is located or there may be also a posterior but closed projection; the style is either bent or straight, the stamens are free from long hairs, the length of spur of stamen varies in different species, and the hairs if present on the spurred petal are straight. This group comprises:

A. Spur of stamen is of the same length as anther cells: *V. ro-*

tundifolia (Fig. 5), *V. Canadensis* (Fig. 6), *V. Nuttallii* (Fig. 7), *V. hastata* (Fig. 8), *V. pubescens* (Fig. 9), *V. scabriuscula* (Fig. 10) and *V. tripartita* (Fig. 11 simple leaved plant; Fig. 12, plant from moist woods).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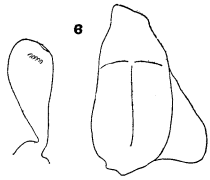
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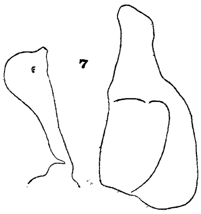
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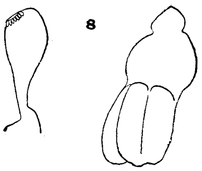
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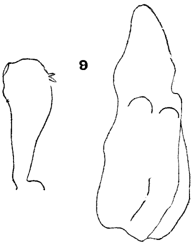
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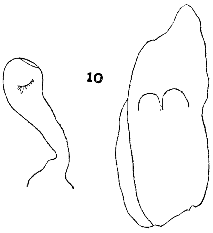
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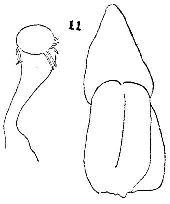
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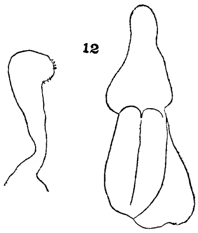
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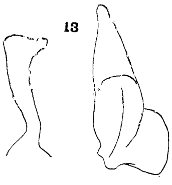
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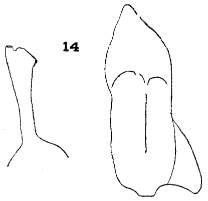
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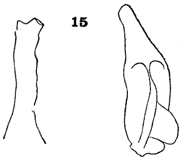
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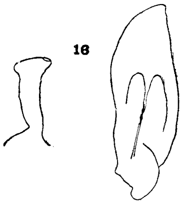
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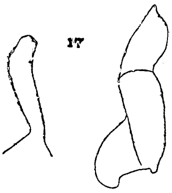
B. Spur of stamen is less than the anther cells in length; *V. blanda* (Fig. 13), *V. primulaefolia* (Fig. 14), *V. lanceolata* (Fig. 15), *V. palustris* (Fig. 16), and *V. renifolia* (Fig. 17).

C. Spur of stamen extends 1.5 to 1.8 mm. below anther cells: *V. pedata* (Fig. 18) and *V. ovata* (Fig. 19).

D. Spur of stamen extends 2.3 to 3.6 mm. below anther cells.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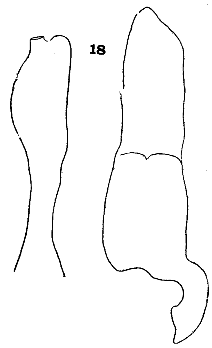
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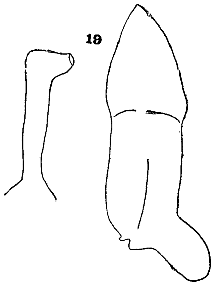
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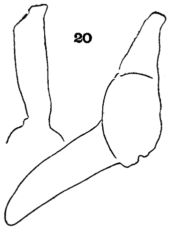
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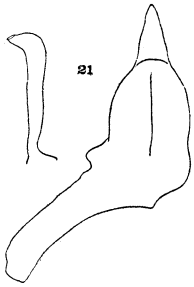
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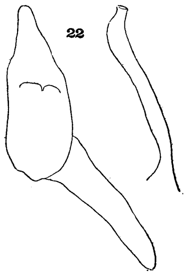
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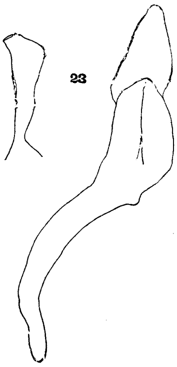
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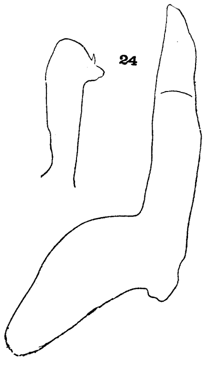
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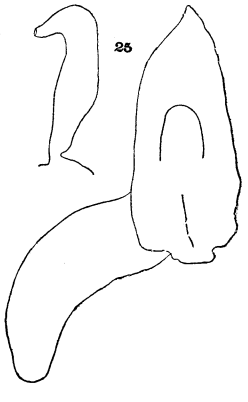
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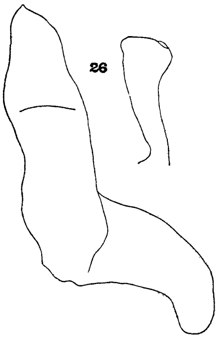
This group may be further subdivided according to the width of spur at its widest portion into:

(*a*) Spur .7 to .8 mm. wide at the widest portion: *V. arenaria* (Fig. 20), *V. Labradorica* (Fig. 21), *V. striata* (Fig. 22) and *V. Selkirkii* (Fig. 23).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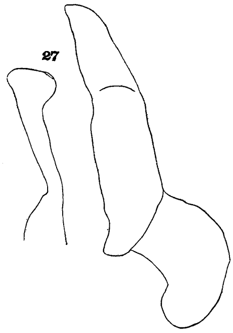
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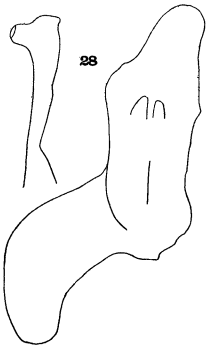
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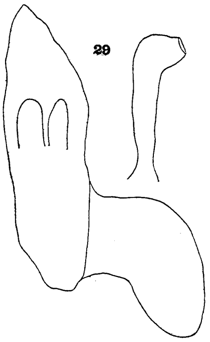
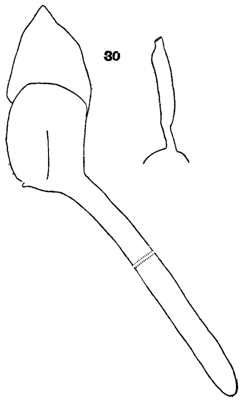

29


30

(*b*) Spur 1.5 to 1.8 mm. wide at its widest portion: *V. delphinifolia* (Fig. 24), *V. odorata* (Fig. 25), *V. obliqua* (Fig. 26), *V. palmata* (Fig. 27), *V. sagittata* (Fig. 28) and *V. sororia* (Fig. 29).

E. In *V. rostrata* (Fig. 30) the length of spur is about 9 mm.

It will be seen that we have in this consideration the grouping of species of the genus into a number of natural groups which further study will no doubt justify. As to whether these groups include hybrids, or varieties of certain species, or each is deserving of the specific rank assigned to it further study alone will demonstrate. It is to be hoped that no more species will be described without a consideration of the morphological features of the genus indicated in this paper. The study of this genus by the author will be continued and he desires to acknowledge his indebtedness to Mr. C. D. Beadle, of Biltmore, N. C., and Mr. C. H. La Wall, of Philadelphia, for some of the material furnished for this investigation; and to Miss Florence Xaple, of Philadelphia, for assistance in certain parts of the work.